

GENERIC PLACEMENT OF *CHAPTALIA HINTONII* (ASTERACEAE: MUTISIEAE)

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ABSTRACT

Chaptalia hintonii, of south-central Mexico, was recently transferred to the otherwise essentially Old World genus *Gerbera* on the basis of the occurrence of staminodes in the pistillate flowers. No clear position within *Gerbera* was determined for the species. In contrast, *C. hintonii* also has been placed among the eight species of sect. *Chaptalia*, based on its similarity in a set of features including scape morphology, head behavior, ray corolla morphology, cypselar vestiture, flower biology, and geography. Other species of South American and Mexican *Chaptalia*, including one other from sect. *Chaptalia*, also are known to produce staminodes, a feature interpreted here as plesiomorphic, either as vestigial occurrence or as the result of developmental intermediacy between bisexual disc florets and outer, pistillate ray florets. The hypothesis that *C. hintonii* belongs with *Chaptalia* is stronger than that for positioning *C. hintonii* in *Gerbera*.

RESUMEN

Chaptalia hintonii, del centro-sur de México, fue transferida recientemente al género esencialmente del Viejo Mundo *Gerbera* en base a la presencia de estaminodios en las flores pistiladas. No se determinó una posición clara en *Gerbera* para la especie. Por contra, *C. hintonii* ha sido colocada entre las ocho especies de la sect. *Chaptalia*, en base a su similitud en un conjunto de características que incluyen la morfología del escapo, comportamiento del capítulo, morfología de los radios de la corola, indumento de las cipselas, biología floral, y geografía. Otras especies de *Chaptalia* de Sur América y México, incluida otra de la sect. *Chaptalia*, también se sabe que producen estaminodios, una característica interpretada aquí como plesiomórfica, tanto como ocurrencia vestigial o como resultado de desarrollo intermedio entre flósculos bisexuales del disco y flores radiadas pistiladas. La hipótesis que *C. hintonii* pertenece a *Chaptalia* es más fuerte que la que posiciona a *C. hintonii* en *Gerbera*.

In a recent discussion of the Mexican species *Chaptalia hintonii* Bullock and its relationship to other species groups of Mutisieae-Mutisiinae, Katinas (1998) concluded that *C. hintonii* should be placed in *Gerbera* rather than *Chaptalia*. In contrast, in a revision of the 12 North American and continental Central American species most recently considered to be *Chaptalia*, Nesom (1995) treated *C. hintonii* among the six species of sect. *Chaptalia*. Two additional species from Mexico were added to sect. *Chaptalia* by Cabrera and Nesom (2003). Indeed, the distinction between the New World *Chaptalia* Vent., 1802, and the Old World genus *Gerbera* L., 1758, is not sharply defined, as observed by Jeffrey (1967). Hansen (1990) provided additional perspective on taxonomic problems in the larger generic group of monocephalous, essentially scapose species of

Mutisiinae (the "Gerbera-complex") that includes these two genera and informally suggested a return to earlier positions of Schultz-Bipontinus (1856) and Baillon (1882), who believed that the limits of *Gerbera* should include New World species now treated in *Chaptalia*. Nesom (1995) also noted that recognition of the taxonomic boundary between *Chaptalia* and *Gerbera* is problematic but maintained *Chaptalia* as distinct.

In the observations by Katinas (1998), she did not deal directly with significant considerations pertinent to a judgement of generic placement of *Chaptalia hintonii*—it is among the species that constitute sect. *Chaptalia* (Nesom 1995), and cypselar vestiture suggests that *Chaptalia* has evolved apart from *Gerbera* (Hansen 1990).

Species of sect. *Chaptalia* are characterized by monocephalous, ebracteate or few-bracted scapes, heads nodding in bud, broad, cream-colored rays with a purple midstripe on the abaxial surface, and functionally staminate disc flowers. This set of features apparently does not consistently occur in any other group of Mutisiinae. *Chaptalia tomentosa* Vent., the type of the genus, is native to the Atlantic and Gulf coastal plains of the southeastern United States; the other seven species occur in montane habits in eastern and south-central Mexico. Within the section, three species groups can be recognized: (a) *C. tomentosa* and *C. madrensis* Nesom produce narrowly beaked cypselas and pistillate ray corollas without an inner lip; (b) *C. pringlei* Greene is alone in its heads without a zone of rayless pistillate flowers (all pistillate flowers produce conspicuous rays), and cypselas with a short neck; (c) *C. lyratifolia* Burkart, *C. hidalgoensis* Cabr. & Nesom, *C. mexicana* Burkart, *C. hintonii*, and *C. estribensis* Nesom are similar in their colonial habit from rhizomes, leaves with cordate blades and mucronulate margins, pistillate flowers with relatively short style branches, and unbeaked cypselas. *Chaptalia hintonii* differs from *C. lyratifolia*, *C. hidalgoensis*, *C. mexicana*, and *C. estribensis* primarily in its thicker, more easily disconnected rhizomes, and thinner leaves, but the geographic and morphological coherence of these five species within sect. *Chaptalia* seems apparent. The transfer of *Chaptalia hintonii* to *Gerbera* implies that the species belongs to neither the *C. lyratifolia* group ("group c" above) nor sect. *Chaptalia*, but Katinas's observation on the implied non-cohesiveness of sect. *Chaptalia* is indirect—only through her removal of *C. hintonii*.

"The characteristic lack of staminodes in *Chaptalia* and their presence in *Gerbera*" led [Katinas] to place [*Chaptalia*] *hintonii* in the genus *Gerbera*" (Katinas 1998, p. 380). Also, "*Chaptalia hintonii* is much closer to *Gerbera* in its floral characteristics" (p. 382). She noted that for *C. hintonii*, "all florets bilabiate," "outer ray florets conspicuously surpass the involucre," and "ray florets possess staminodes" were features supporting its removal from *Chaptalia*. Numerous other species of *Chaptalia*, however, have all florets bilabiate, all species of sect. *Chaptalia* have large outer rays (e.g., see numerous published pho-

tographs of *C. tomentosa*), and staminodes also occur in the inner pistillate flowers of at least three other Mexican species: *C. estribensis* (sect. *Chaptalia*) from the locality in Oaxaca, but not from the localities in Hidalgo; *C. texana* Greene (sect. *Leria* (DC.) Burkart) in plants of Baja California Sur but apparently not from mainland localities; and *C. hololeuca* Greene (sect. *Leria*) from one locality in Coahuila but not from others. Similar staminodes also occur sporadically in both the outer and inner pistillate flowers of the South American species *C. incana* Cuatr., a species suggested by Cuatrecasas (1961) to belong in sect. *Leria* (DC.) Burkart. Finally, Burkart (1944) viewed a group of cordate-leaved South American *Chaptalia* species as better placed in *Trichocline* Cass. than *Chaptalia*, particularly in view of their production of staminodes in the outer pistillate florets. Jeffrey (1967) and Hansen (1990) found that pappus texture and cypselar vestiture refer these species to *Chaptalia* rather than to *Trichocline* or any group of the *Gerbera*-complex.

Parallel variation in the production of staminodes is found in Old World *Gerbera*. Katinas, following Hansen (1990), noted that a reduction to vestigial staminodes has occurred in several groups of *Gerbera* and that they are completely absent in *Gerbera* sect. *Parva* H.V. Hansen.

Hansen (1990) and Nesom (1995) have observed that the inner pistillate florets in *Chaptalia* are intermediate between the disc florets and the outer ray florets. "The inner pistillate flowers of *Chaptalia* appear to be transitional between the ligulate, outer, pistillate ones and the tubular, inner, bisexual flowers in two ways: 1) they usually are bilabiate, even if the outermost are not, and 2) in some species they sporadically produce small, abortive stamens [staminodes]" (Nesom 1995, p. 155). The occurrence of staminodes in *Chaptalia* and other entities of the *Gerbera*-complex is a plesiomorphic feature (Hansen 1990)—they may be interpreted as vestigial organs or as developmentally intermediate in origin (as above). A plesiomorphic similarity between Mexican *C. hintonii* and certain groups of Old World *Gerbera* does not imply closeness of relationship.

What genus?

Evidence at hand indicates that *Chaptalia hintonii* belongs in the same genus as *C. tomentosa*, the type species of *Chaptalia*. If *C. hintonii* is to become a species of *Gerbera*, then so also must the type and at least the other species of sect. *Chaptalia*. Most of *Chaptalia* as a genus holds together well. Species of sects. *Leria* (DC.) Burkart (*C. nutans* Polak., the type), *Archichaptalia* Burkart (*C. rotundifolia* D. Don, the type), and *Pseudotrichocline* Burkart (*C. isernina* Cuatr., the type) are similar to those of sect. *Chaptalia* in their nodding buds and cypselar vestiture, which provides evidence for the phylogenetic coherence of *Chaptalia* apart from Old World members of the *Gerbera*-group.

"Almost all taxonomic main groups [of the *Gerbera*-complex] can be circumscribed by having a special type of achene (cypselar) hair" (Hansen 1990, p.

471). *Chaptalia* has "achene hairs as in *Gerbera* sect. *Piloselloides* Less. but more narrow and either much smaller or much longer and then less inflated" (p. 476, Table 4). Katinas (p. 382) noted that "the species of section *Piloselloides* seem to be the most closely related [to *Chaptalia*] by virtue of the length of the outer ray florets and the type of pubescence on the cypselas ..." but her Table 1 and related comments do not indicate that the cypselar pubescence in these two groups is identical. There is slight variation among cypselar hairs within sect. *Chaptalia*, but I find the vestiture of *C. hintonii* indistinguishable from that of other species of the *C. lyratifolia* group.

Chaptalia sects. *Chaptalia*, *Leria*, and *Archichaptalia* are overlapping in morphological features—leaf shape, degree of elaboration of bracts on the scape, presence/absence of inner pistillate florets, style morphology, elaboration of the inner lip of pistillate florets, ray size, and degree of elaboration of cypselar beak. Especially in their long-petiolate, cordate leaves and broad rays, species of sect. *Archichaptalia* are similar to those of the *Chaptalia lyratifolia* group of sect. *Chaptalia*. Even the distinctive ovarian sterility of the central florets of sect. *Chaptalia* is not a totally exclusive feature. A Brazilian species (Dias de Moraes 1998) is said to be most closely similar to species of sect. *Archichaptalia*, but it apparently is anomalous there in its functionally staminate disc florets (as well as lack of inner pistillate florets, ebracteate scapes, all characters found in some species of sect. *Chaptalia*, where the Brazilian species might technically be placed). Cuatrecasas (1965) described variation in fertility between heads of different plants of the Peruvian *C. malcabalensis* Cuatr.: one head with outer radiate pistillate florets and bisexual fertile central florets, lacking inner rayless pistillate florets; another head with outer radiate pistillate florets, inner rayless pistillate florets, and central florets with sterile ovaries, except for two florets with fertile ovaries and sterile anthers.

Chaptalia sect. *Lieberkuhna* (Cass.) Burkart (*C. piloselloides* (Vahl) Baker, the type) and sect. *Loxodon* (Cass.) Burkart (*C. excapa* (Pers.) Baker, the type), as a combined group, stand apart from all the rest of *Chaptalia* in production of erect buds, potential for cleistogamous heads, and distinctive cypselar vestiture, and it is possible that this small group of species will be separated at generic rank. This group apparently is the one underlying Hansen's notice (1990) that *Chaptalia* is separable into two groups, based on morphology of cypselar hairs. The Antillean group sect. *Microchaptalia* Burkart appears to be heterogeneous, but I agree with Burkart (1969) that all of it belongs with true *Chaptalia*, rather than being divided between *Chaptalia* and *Lieberkuhna*, as suggested by Jeffrey (1967).

Katinas found similarities between *Chaptalia hintonii* and *Gerbera* sects. *Lasiopus* (DC.) Schultz-Bip., *Pseudoseris* (Baillon) C. Jeffrey, and *Piloselloides* Less. (= *Piloselloides* (Less.) C. Jeffrey), although the species did not fit within any of them. In Hansen's strict consensus tree for the *Gerbera*-complex (1990), these three groups are most closely related to *Chaptalia* and phylogenetically sepa-

rate from *Gerbera* sensu stricto, which is the basal OTU in the whole *Gerbera*-complex and separated from *Chaptalia* by *Leibnitzia* Cass., *Perdicium* L., and others. Thus the transfer of *C. hintonii* to *Gerbera* appears equivalent to a step toward recognizing the whole *Gerbera*-complex as a single genus rather than a precise hypothesis of relationship.

The ultimate fate of all of *Chaptalia* may be to join a much broadened *Gerbera*, as suggested by Hansen and earlier botanists, or it may be maintained (perhaps disjoined from *Lieberkuhna*) among a group of smaller genera, as suggested by Jeffrey, but the taxonomic decision in either case should be made in a broad perspective. The taxonomic segregation of *C. hintonii* has little support compared to the geographic and morphological coherence of this species with *Chaptalia* sect. *Chaptalia* and the apparent phylogenetic unity of most of the whole genus *Chaptalia*.

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